

A NEW SPECIES OF *APHYLLON* (OROBANCHACEAE) PARASITIC ON *GALIUM* IN THE WESTERN USA

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ABSTRACT

Aphyllon epigalium Colwell & A.C. Schneid. is described as a new species from Oregon and California. This taxon is distinguishable from the other members of *Aphyllon* Mitch. sect. *Aphyllon* in Western North America (i.e., *A. fasciculatum* [Nutt.] Torr. & A. Gray, *A. purpureum* [A. Heller] Holub, and *A. uniflorum* [L.] Torr. & A. Gray) in its host preference for *Galium* L., by having 2–4 yellow flowers per stem, and pedicels longer than the stem. Two subspecies are described: *Aphyllon epigalium* subsp. *epigalium*, which occurs in the Cascade and Klamath ranges in Oregon and California, and the Coast Ranges and Sierra Nevada in California; and *A. epigalium* subsp. *notocalifornicum* Colwell & A.C. Schneid., currently known from few sites in montane southern California. The new subspecies differ from one another in flower size, corolla lobe shape, host preference, geographic range, and nuclear and plastid genetic markers. An updated key to California and Oregon *Aphyllon* sect. *Aphyllon* is presented.

Key Words: *Aphyllon epigalium* subsp. *epigalium*, *Aphyllon epigalium* subsp. *notocalifornicum*, *Galium*, *Gymnocaulis*, *Orobanche*, Orobanchaceae, parasite, taxonomy.

For the past century, the concept of *Aphyllon* Mitch. sect. *Aphyllon* (formerly *Orobanche* L. sect. *Gymnocaulis* Nutt., see Schneider 2016) has included just two species, *A. uniflorum* (L.) A. Gray and *A. fasciculatum* (Nutt.) Torr. & A. Gray, both of which have large ranges in North America and occupy a variety of habitats and floristic regions. Previous efforts to segregate additional western North American taxa (Suksdorf 1900, 1906, Achey 1933) were not widely accepted. Recently, a combination of host-relationship, morphological, and molecular evidence has been used to distinguish the western North American populations of *A. uniflorum*, recognized under the name *A. purpureum* (A. Heller) Holub (Schneider 2016). Sufficient accumulation of herbarium specimens for analyses, coupled with phylogenetic evidence provided by Schneider et al. (2016) make it possible to convincingly parse this species complex into additional natural groups.

Within the California Floristic Province, both *A. purpureum* and *A. fasciculatum* display variability in coloration, size, number of flowers, and host preference. We here describe and name a distinctive entity in this region that has been noted informally as appearing intermediate between *A. purpureum* and *A. fasciculatum* by several earlier collectors. For example, in 1918, W. L. Jepson added the following annotation to his specimen 6385 (JEPS 10829), collected three years earlier and determined as *A.*

fasciculatum: “This has the habit of *O. uniflora* but the calyx segments are broad as in *O. fasciculata*. Moreover the color of the flowers is yellow as per note in Field Book. A specimen similar to this, Comptche, Harriet Walker 368, is in UC. Herb.” (Notes: Walker 368 is UC 112774; the entry in Jepson Field Notebook for 6385 can be found here: http://ucjeps.berkeley.edu/cgi-bin/display_fb.pl?page_no=31_89.) In 1956, G. Thomas Robbins put the following note on several specimens at CAS (Follette s.n., 1930, Howell 19834, Howell 21000): “In habit (particularly the reduced number of scapes) these plants suggest *O. uniflora*, but they have the broader calyx-lobes & the more pointed, non-ciliolate corolla-lobes of *O. fasciculata*.” Two decades later, in her master’s thesis on *Orobanche* sect. *Gymnocaulis* (Watson 1975), the second author of this paper described and proposed this entity as a subspecies of *Orobanche fasciculata* Nutt., but the name was not formally published.

Based on the distinct morphology and ecology of these plants, presented below, and with support from the molecular phylogenetic analyses previously cited, we conclude that plants parasitic on *Galium* L. in the western United States form a monophyletic group distinct from other previously described species, but sympatric with them. Furthermore, these *Galium* parasites warrant division into two subspecies

distinguishable by host preference, morphology, geographic range, and genetic distinctness.

TAXONOMIC TREATMENT

Aphyllon epigalium Colwell & A.C. Schneid., sp. nov. (Fig. 1) —TYPE: USA, California, Butte Co., Paradise, Elliot Rd, 39.7592 N, 121.5968 W, host *Galium bolanderi* A. Gray, 1 June 1974, K. D. Cox 188 (holotype: JEPS; isotypes: CHSC, SD).

Diagnosis: Distinct from all other species of *Aphyllon* in parasitizing *Galium* spp., and from other Western U.S. species of *A.* sect. *Aphyllon* in having a combination of both 2–4 yellow flowers per stem and pedicels longer than the stem (the combined vegetative and inflorescence axis).

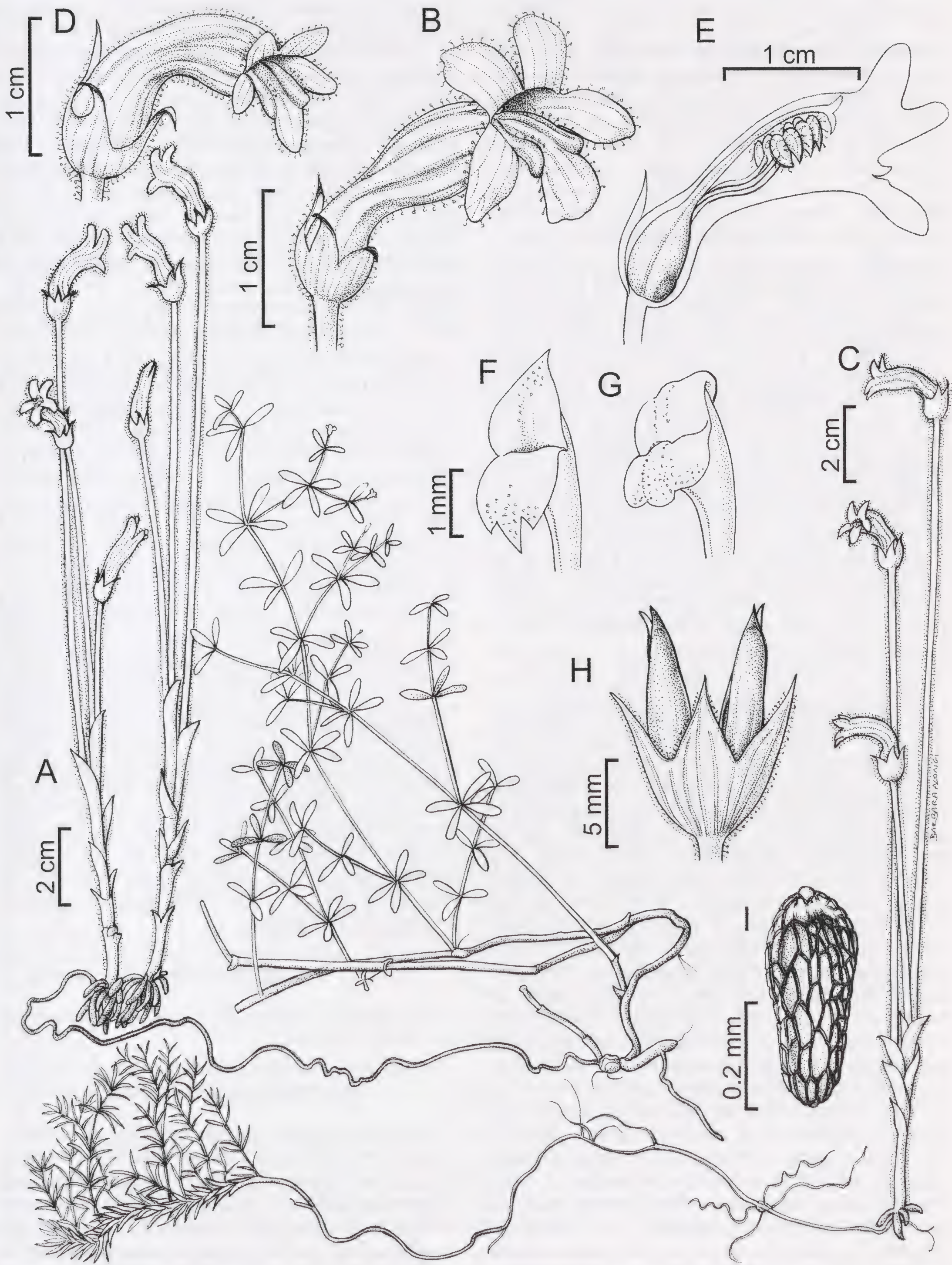
Plants annual or overwintering annual, 10–30 cm in length. **Roots** few to many, blunt, simple, succulent, up to 1 cm in length, often forming a mass around host attachment (primary haustorium), rarely with secondary haustoria. **Stem** unbranched or few-branched from basal host attachment point, succulent but slender and evenly thickened, 2–5 mm diameter. Stem length (from belowground host attachment point to terminus of inflorescence axis at ground level) 1–15 cm. Belowground structures glabrous, pallid; aboveground structures moderately to densely glandular-pubescent, straw-color to bright yellow, often tinged pinkish to purplish. **Leaves** few (these plus inflorescence bracts 2–10[–15] in number), reduced to scales 5–9 mm long, to 9 mm wide at broadest point, deltoid to linear, loosely imbricate or not overlapping, clasping stem, tips subacute to truncate, margins entire, glabrous. **Inflorescence** axis is a continuation of the vegetative stem, arising just below the soil surface. Flowers axillary, one per bract, (1–)2–4 per stem (in clustered or branched plants flowers appearing to be more numerous), the distal flower usually smaller than others, or aborted. **Bracts** 5–15 mm, intergrading with the reduced scale-leaves below inflorescence but trending larger, oblanceolate to obovate, loosely clasping, sometimes recurved at tip. **Pedicels** (6–)10–21 cm, erect; bracteoles 0. Proximal pedicels longer than the stem, distal pedicels sometimes not. **Calyces** (4–)5–11 mm, suberect, often purplish-tinged distally, sometimes entirely pinkish to reddish-purple, glandular-pubescent. Sepals fused at base into cup 3–7 mm deep, subequally divided distally into 5 narrowly triangular to subulate lobes 2–4 mm long, 1–3 mm wide. **Corollas** 13–30 mm, fused into a curved tube, constricted above ovary, then slightly inflated adaxially, narrowing at mouth, moderately glandular

pubescent; interior straw-colored to yellow, exterior similar, or pinkish, or tinged reddish, purplish, or finely purple-veined. Palatal folds evident, concolor or yellow, sparsely glandular-pubescent, inward-pouched between all but upper two lobes. Corolla lobes five, 2–4 mm long, 1–4 mm wide, similar in color to tube, oblong to obovate, erect to spreading and recurved at tip, more strongly so in age, tip margins rounded, truncate, minutely notched or apiculate, sparsely glandular pubescent. **Stamens** didynamous, with glabrous filaments; anther sacs villose-tomentose from longitudinal suture, glabrous on back, clustered below stigma. **Stigma** white, two-lobed, the lobes thin, triangular, usually with one or two subsidiary teeth, becoming recurved and thickened in age, included within corolla tube. **Ovary** two-chambered, placentation parietal, with orange-pigmented gland at abaxial base. **Capsules** 6–12 mm, ovoid to oblong-ovoid, dehiscent. **Seeds** 0.2–0.4 mm, brown, irregularly faceted, ovoid to oblong, most 2–3× longer than wide, surface favose.

Aphyllon epigalium* subsp. *epigalium Corolla yellow, often with reddish or purplish tinge or purplish venation externally, (17–)20–30 mm long, tube moderately arched such that flowers are suberect, with mouth of open flower presented at 45°, corolla lobes less than twice as long as wide, spreading and/or recurved as the flower matures

Paratypes: USA, CALIFORNIA, **Butte Co.:** Hills, June 1879, *Austin s.n.* (NY); Little Chico Canyon, May 1896, *Bruce* 828 (MO); Marysville Buttes, Rocky Slope of East Butte, 16 May 1902, *Heller s.n.* (NY); Jonesville, rocky crest of ridge between Willow and Colby Creeks, host *Galium bolanderi*, 10 June 1931, *Copeland* 1557 (CAS, RSA); north fork of the Feather River above Camp Rogers, on trail to Buck's Lake, 22 May 1957, *Balls* 22511 (RSA); Doon Grade, near Paradise, 19 May 1970, *Ahart* 55 (CHSC); Big Butte Creek, 11 May 1972, *Salinas* 2 (CHSC); Bluffs on E side of Humbug Rd., 2 mi NE of Centerville, 18 April 1980, *M.S. Taylor & Jokerst* 2539 (CHSC); Chino Ridge, host *Galium bolanderi*, 29 May 1981, *M. S. Taylor* 3814 (JEPS); Potter Ravine, 2 1/2 mi NE of Oroville Dam, *Ahart & Jokerst* 4961 (CAS, CHSC); Lake Oroville Recreation Area, Dan Beebe Trail, host *Galium porrigens* Dempster var. *tenue* (Dempster) Dempster, 13 May 1991, *Oswald & Ahart* 4585 (CHSC, UC); Lime Saddle Memorial Park, host *Galium porrigens* var. *tenue*, 15 May 1991, *Oswald* 4596 (CHSC); 1.5 mi ENE of Feather Falls, *Castro et al.* 513 (CHSC); Jackson Ranch Ridge, 0.9 mi ENE of Feather Falls, 1 June 1995, *Janeway* 4765. **Contra Costa Co.:** Mt.

FIG. 1. Illustration of *Aphyllon epigalium*. A–B. *A. e.* subsp. *epigalium*. A. Habit and connection to its host, *Galium bolanderi*. B. Fully open flower. C–D. *A. e.* subsp. *notocalifornicum*. C. Habit and connection to its host, *Galium andrewsii*. D. Fully open flower. E. Longitudinal bisection of typical flower, showing arrangement of stigma, anther sacs, and gland at base of ovary. F. Oblique frontal view of typical stigma at early anthesis showing a toothed lower lobe. G. Oblique frontal view of typical stigma at late anthesis showing thickened, recurved lobes. H. Dehiscent capsule. I. Mature seed, showing surface



reticulation. Illustration by Barbara Alongi. Source material: Parasite in A–B drawn from *Oswald & Ahart* 4585 specimen (UC 1586604), host plant in A from *Powell* 2790 (JEPS 82506), parasite and host in C–D from *Bell* 159 specimen (RSA 598503), E–G from a composite of *Mason* 12308 specimen (UC 1179027) and live material from *Schneider* 1029 and 1033 (JEPS, SBBG), H & I from *Jepson*, *s.n.*, Sisson specimen (JEPS 10831).

Diablo, Russelmann Park, host *Galium nuttallii* A. Gray, 16 May 1935, *Bowerman* 2995 (UC). **El Dorado Co.:** Placerville, 3 May 1941, *Reed s.n.* (UC); Placerville, 30 April 1943, *Robbins* 1050 (UC); 3 mi east of Placerville, host *Galium nuttallii*, 24 May 1944, *Robbins* 1632 (CAS, UC). **Humboldt Co.:** Jarinyan's, 12 July 1888, *Chestnut & Drew s.n.* (UC); Brannan Mountain, ridge north of Willow Creek, 7 July 1911, *Tracy* 3422 (UC). **Lake Co.:** April 1930, *Follette s.n.* (CAS); Eel River watershed, 21 June 1932, *Benson* 3725 (RSA); Four miles above Lucerne, host *Galium californicum* Hook. & Arn., 2 May 1936, *Mason* 11099 (GH, RSA, UC); Bartlett Mountain, 22 May 1940, *Mason* 12308 (UC, WS); Bartlett Mountain, Sawmill Flat, host *Galium californicum*, 18 June 1945, *Howell* 21000 (CAS, MO). **Madera Co.:** Upper Mariposa Grove, Yosemite Park, host *Galium bolanderi*, 19 July 2010, *Colwell* 10-107 (YM). **Mariposa Co.:** Turtleback Dome access road, Yosemite Park, host *Galium porrigens*, 9 June 2007, *Colwell* 07-56 (UC, YM). **Mendocino Co.:** Near Comptche, 23–29 June 1906, *Walker* 368 (UC); Round Valley, May 1954, *Irwin s.n.* (CAS); Confluence of Elder Creek with the South Fork of Eel River, 23–24 June 1961, *Sharsmith* 4876 (UC); Montgomery Woods State Natural Reserve, along Orr Springs Road, host *Galium muricatum* W. Wight, 28 May 2007, *Warner* 86 (JEPS). **Monterey Co.:** Monterey, *s.d.*, *Abbott s.n.* (CAS). **Napa Co.:** SR 37, 20 miles southwest of Monticello Dam, 12 May 1961, *Wardell* 27 (ARIZ, WTU). **Nevada Co.:** Alpha Road 1/2 mile north of Skillman Flat on Highway 20, 10 June 1965, *True* 2036 (CAS). **Placer Co.:** 1 mile west of Baxter, 7 May 1940, *Hitchcock* 6349 (WTU). **Plumas Co.:** Indian Valley, 1872, *Ames s.n.* (NY); *no locality, s.d.*, *Austin s.n.* (E); Greenville, 1 July 1924, *Stephens* 8329 (SD); Ridge NE of Humbug Valley, 7 June 1951, *Quick* 51-97 (CAS); Greenhorn Creek, 24 May 2004, *Ahart* 10948 (CHSC, JEPS). **Shasta Co.:** Castle Crag Trail, June 1893, *Dudley s.n.* (CAS); Burney, host *Galium bolanderi*, 30 May 1923, *Bettiel s.n.* (CAS); 25 miles east of Redding, 20 May 1940, *Hitchcock* 6493 (WTU); East of Burney, 23 May 1941, *Cantelow s.n.* (CAS); Whiskeytown Lake, 29 May 1971, *Ganley* 640 (RSA); 2 miles south of Sweetbrier, 10 June 1980, *M. S. Taylor* 2816 (CHSC, JEPS); Clear Creek, 2.5 mi WSW of Clear Creek Rd and business I-5, host *Galium porrigens* var. *tenue*, 6 May 1981, *Powell* 2790 (JEPS); Hwy 299, 9 mi N of Redding, 9 May 1993, *Wisura* 4886 (RSA); Hamp Creek, 0.3 mi W of Ponderosa Way, 25 May 1993, *D. W. Taylor* 13501 (JEPS, RSA); Shasta Lake, Klikapudi Trail, host *Galium bolanderi*, 6 May 1994, *Oswald & Ahart* 6163 (CHSC, JEPS). **Siskiyou Co.:** Upper Sacramento, Hillside near Sisson, 24 July–10 Aug 1894, *Jepson s.n.* (UC); Black Butte, along Hwy 99, south of Weed, 22 June 1958, *Chisaki & Newcomb* 1154 (NY, UC, WS, WTU); Vicinity of Beaver Creek Basin, Siskiyou National Forest, 12 July 1944, *Dunkle* 9086 (RSA). **Sonoma Co.:** Armstrong Woods Park, 17 May 1976, *Harrison s.n.*

(JEPS). **Tehama Co.:** Between Mineral and Paynes Creek, 26 May 1927, *Grinnell s.n.* (JEPS); Log Spring Ridge, 9 July 1941, *Eastwood & Howell* 9730 (CAS); W of Paskenta near 15 mile post, host *Galium ambiguum*, 21 June 1953, *Baker & Wagnon* 12775 (RSA, UC). Brokeoff Mountain Trail, Lassen Volcanic National Park, host *Galium grayanum* Ehrend., 4 August 1986, *Oswald* 2267 (CHSC); Ides Cove Loop Trail, Long Lake, host *Galium ambiguum* W. Wight, 12 July 1988, *Oswald* 3552 (CHSC); Plum Creek Rd. SE of the town of Paynes Creek, host *Galium porrigens* var. *tenue*, 14 May 1997, *Oswald & Ahart* 8415 (CHSC); Off Hwy 32, 2 miles west of campground on Deer Creek, *Fischer* 835 (CHSC). **Trinity Co.:** Musser Hill, 25 May 1914, *Yate* 354 (RSA); North Yolla Bolly Mountains, Grasshopper Camp, 17 July 1951, *Munz* 16599 (RSA); 1 air mile SW of Mt. Eddy, Middle Deadfall Lake, 1 Aug 1971, *Heckard & Rubtsoff* 2696 (JEPS). **Tuolumne Co.:** South fork Stanislaus River, Italian Bar, 5 June 1915, *Jepson* 6385 (JEPS); Sonora, five miles east on Hwy 120, 19 May 1957, *Dodge* 172 (ARIZ), Big Oak Flat Road at lower end of Tuolumne Grove, Yosemite Park, host *Galium bolanderi*, 8 July 2004, *Colwell & Coulter* 04-83 (YM). **OREGON, Curry Co.:** Rogue River, near Hick's Creek, 21 June 1917, *Peck* 7239 (CAS, OSC); Mule Creek, 4 June 1928, *Leach* 1764 (OSC); Paradise Bar, 4 June 1917, *Nelson* 1367 (GH); W of Carpenterville, host *Galium* sp., 5 June 1929, *Henderson* 10157 (OSC); Bear Camp Pasture, 15 July 1978, *Stansell s.n.* (OSC). **Douglas Co.:** Rattlesnake Mountain, Umpqua National Forest, host *Galium oreganum* Britton, 27 July 2007, *Harvey s.n.* (OSC); SE of Steamboat, Umpqua National Forest, 14 July 2008, *Carr* 1559 (OSC). **Jackson Co.:** Sykes Creek, 26 May 1892, *Hammond* 320 (MO). **Josephine Co.:** Coast Mountains, Fortieth Parallel, 8 June 1884, *Howell* 242 (OSC). **Lane Co.:** H. J. Andrews Experimental Forest, host *Galium oreganum*, 16 Aug 1979, *Fitz* 1731 (HJAEF, scan of specimen reviewed for this study).

ETYMOLOGY

This species is named for its parasitic association with *Galium* species.

DISTRIBUTION AND ECOLOGY

Aphyllon epigalium subsp. *epigalium* is found in isolated populations over a large area, from southern Lake County, Oregon, to Madera and Contra Costa counties in California, with a single early record from Monterey County, CA (*Abbott s.n.*) (Fig. 3). This range includes sites in several ecoregions (Griffith et al. 2016), the Cascades and Klamath Mountains of both Oregon and California, the Coast Range, Central California Foothills and Coastal Mountains, Sierra Nevada, and Central California Valley (Sutter Buttes) in California.

Aphyllon epigalium subsp. *epigalium* flowers from late April to July, occasionally in August at higher elevations and higher latitudes. It occurs in light shade of open forest understory or brushy slopes in oak woodland, yellow pine forest, mixed conifer forest, red fir forest, and (rarely) exposed subalpine slopes (Fig. 2H). It has been found over an elevation range of 150–2650 m in foothill to montane zones on a variety of substrates, including igneous, metamorphic and serpentine, typically in the presence of a substantial duff layer.

Reported and observed host plants for this subspecies include *Galium ambiguum*, *G. bolanderi*, *G. californicum*, *G. grayanum*, *G. muricatum*, *G. nuttallii*, *G. oreganum*, *G. porrigens* var. *tenue*, and *G. sparsiflorum* W. Wight subsp. *sparsiflorum*.

***Aphyllon epigalium* subsp. *notocalifornicum* Colwell & A.C. Schneid. subsp. nov. (Fig. 1) — TYPE:** USA, California, Riverside Co., Cleveland National Forest, Agua Tibia Wilderness, NE face of Eagle Crag, SE of the Crosley Saddle, South of the Cutca Trail, host *Galium andrewsii*, 15 June 1995, *Darin Banks 689 & Steve Boyd* (holotype: RSA; isotype: SD).

Diagnosis: *Aphyllon epigalium* subsp. *notocalifornicum* is distinct from *A. epigalium* subsp. *epigalium* in its paler, straw-colored flowers, often with a pinkish cast externally, its shorter corolla length of 13–20(–25) mm, its tube more prominently arched, with the corolla mouth presented $\pm$ horizontally, its narrower corolla lobes (length $2\times$ width) that are either erect or weakly recurved at tips.

Paratypes: USA, CALIFORNIA. **San Bernardino Co.:** Mill Creek, June, *s.d.*, *Smith s.n.* (UC); **San Diego Co.:** Public Camp south of Cuyamaca Lake, 15 June 1937, *Roos 1466* (POM, UCR); Palomar Mountain, Fry Creek Campground, 29 June 1995, *Bell & Clemons 159* (RSA, SD); Agua Tibia Mountains, NE Face of Eagle Crag, 22 June 2016, *Schneider 1029* (topotype, JEPS). **Ventura Co.:** Divide Peak, Ocean View Trail, 16 June and 2 July 1948, *Pollard s.n.*, (CAS, RSA); Santa Ynez Mountains, Ocean View Trail near Divide Peak, 24 June 2016, *Schneider 1033* (JEPS, SBBG).

ETYMOLOGY

This subspecies is named for its distribution within the southern California Floristic Province.

DISTRIBUTION AND ECOLOGY

The known range of *Aphyllon epigalium* subsp. *notocalifornicum* is restricted to the Southern California Mountains ecoregion, specifically the Transverse and Peninsular Ranges in San Bernardino, Ventura and San Diego Counties.

Aphyllon epigalium subsp. *notocalifornicum* flowers from late May to early July. It occurs in light shade and open understory of slopes or riparian areas in oak woodland and conifer forest (e.g., *Pseudotsuga*

macrocarpa [Vasey] Mayr woodland); sometimes in patches of forest within chaparral (See Fig. 2G, I). It occurs over an elevation range of 1200–1500 m.

Specimens cited above report only a single species as the host, *Galium andrewsii* A. Gray, with the exception of two specimens examined (*Smith s.n.*, and *Pollard s.n.*), which do not mention a host.

DISCUSSION

Evolutionary Relationships

A recent molecular phylogenetic study of *Aphyllon* (Schneider et al. 2016) confirmed the existence of several strongly supported host-specific lineages in *A. sect. Aphyllon*. A clade comprising seven samples of *A. epigalium* was sister to a clade of *A. fasciculatum* parasitic on a variety of hosts, including *Eriogonum*, *Eriodictyon*, *Eriophyllum*, and *Phacelia* (Fig. 4), with an estimated divergence of 2 million years ago (A. C. Schneider, unpubl. data). A pair of samples representing the disjunct populations in southern California (= *A. epigalium* subsp. *notocalifornicum*) formed a strongly supported clade sister to the remaining five samples (= *A. epigalium* subsp. *epigalium*), providing additional evidence that the southern California populations are sufficiently distinct to merit recognition at the subspecific level.

Host Relationships

All confirmed hosts of *Aphyllon epigalium* belong to the genus *Galium*, and, with the exception of *G. oreganum* and *G. grayanum*, belong to a single clade of fleshy-fruited *Galium* found from Oregon to Baja California (clade 1 [*Galium* sect. *Baccogalium pro parte*] of Soza and Olmstead 2010). Strong host fidelity such as this is a widespread trait within the holoparasites of the Orobanchaceae, with some significant exceptions among weedy species of *Orobanche* and *Phelipanche* Pomel (Schneeweiss 2007). A large body of literature is devoted to the mechanisms of interaction between Orobanchaceae parasites and their hosts that result in host specificity or host shifts (Höniges et al 2012; Joel et al. 2013; reviewed in Fernández-Aparicio et al. 2016).

Host associations among species of *Aphyllon* have been long noted by taxonomists (Beck-Mannagetta 1890, Munz 1959, Heckard 1973), but recent treatments, benefiting from more extensive host assessments in the field, and more specimens with accurate ecological detail attached, have been able to define host associations more narrowly (Ellis et al. 1999, Collins et al. 2009, Colwell and Heckard 2012, Collins and Yatskievych 2015, Colwell and Yatskievych 2016). Molecular analyses have also highlighted the evolutionary importance of host specificity and corroborate the use of host identity in distinguishing morphologically similar taxa (Schneeweiss 2007, Thorogood et al. 2008, Schneider et al. 2016).

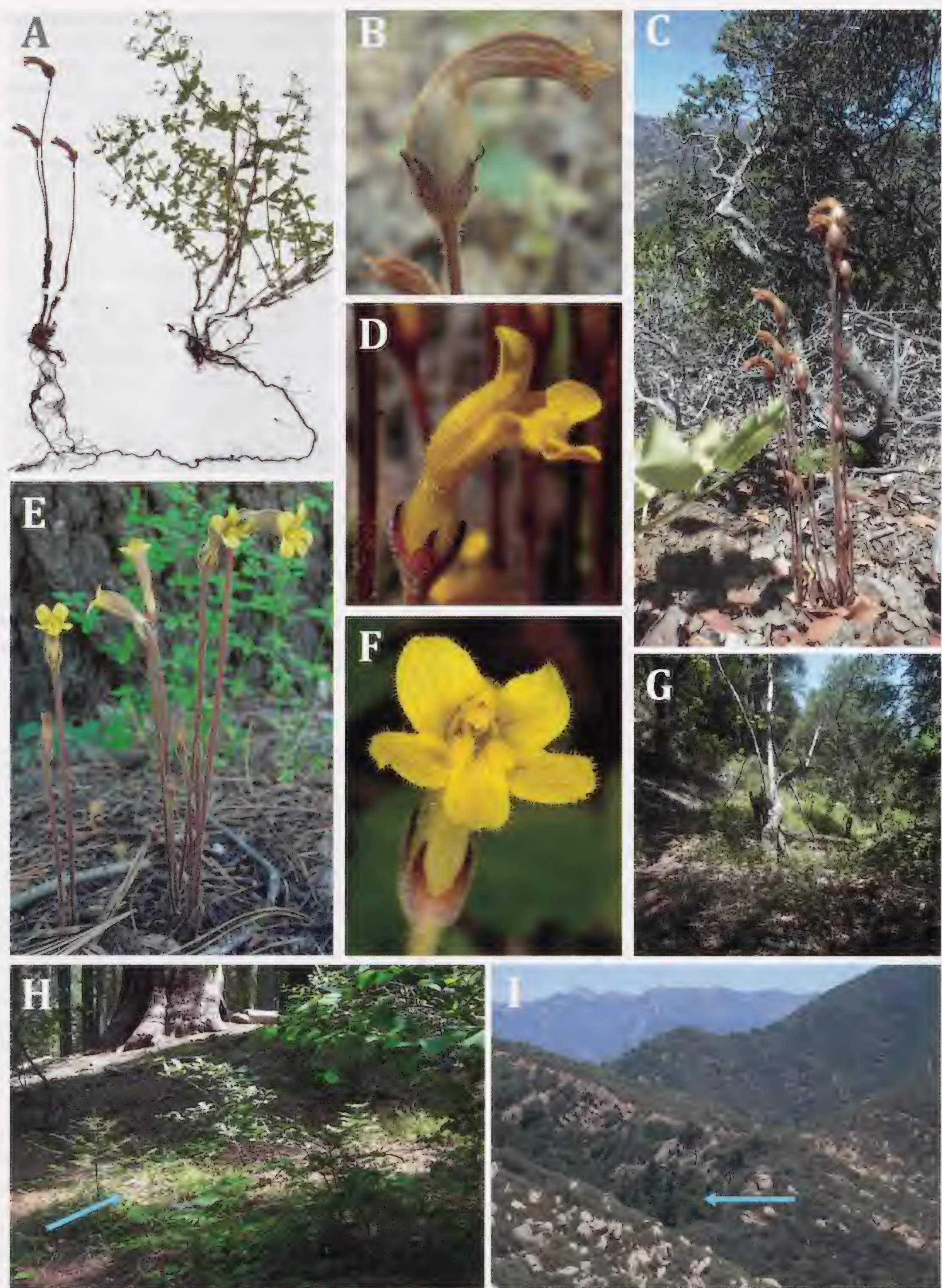


FIG. 2. Morphology and habitat of *Aphyllon epigalium*. *Aphyllon epigalium* subsp. *epigalium* (A, D–F, H). *Aphyllon epigalium* subsp. *notocalifornicum* (B–C, G, I). A. *Aphyllon epigalium* subsp. *epigalium* attached to a root of its host, *Galium sparsiflorum* subsp. *sparsiflorum* (Colwell & Coulter 04-83, YM). B. *Aphyllon epigalium* subsp. *notocalifornicum* flower at late anthesis, ovary beginning to swell (topotype, Schneider 1029, JEPS). C. Several plants of *Aphyllon epigalium* subsp. *notocalifornicum* at late anthesis/early fruit (Schneider 1033, JEPS, SBBG). D. *Aphyllon epigalium* subsp. *epigalium* flower at anthesis, lateral view (Siskiyou Field Institute, Josephine Co., OR. Photo courtesy Keir Morse). E. Several plants of

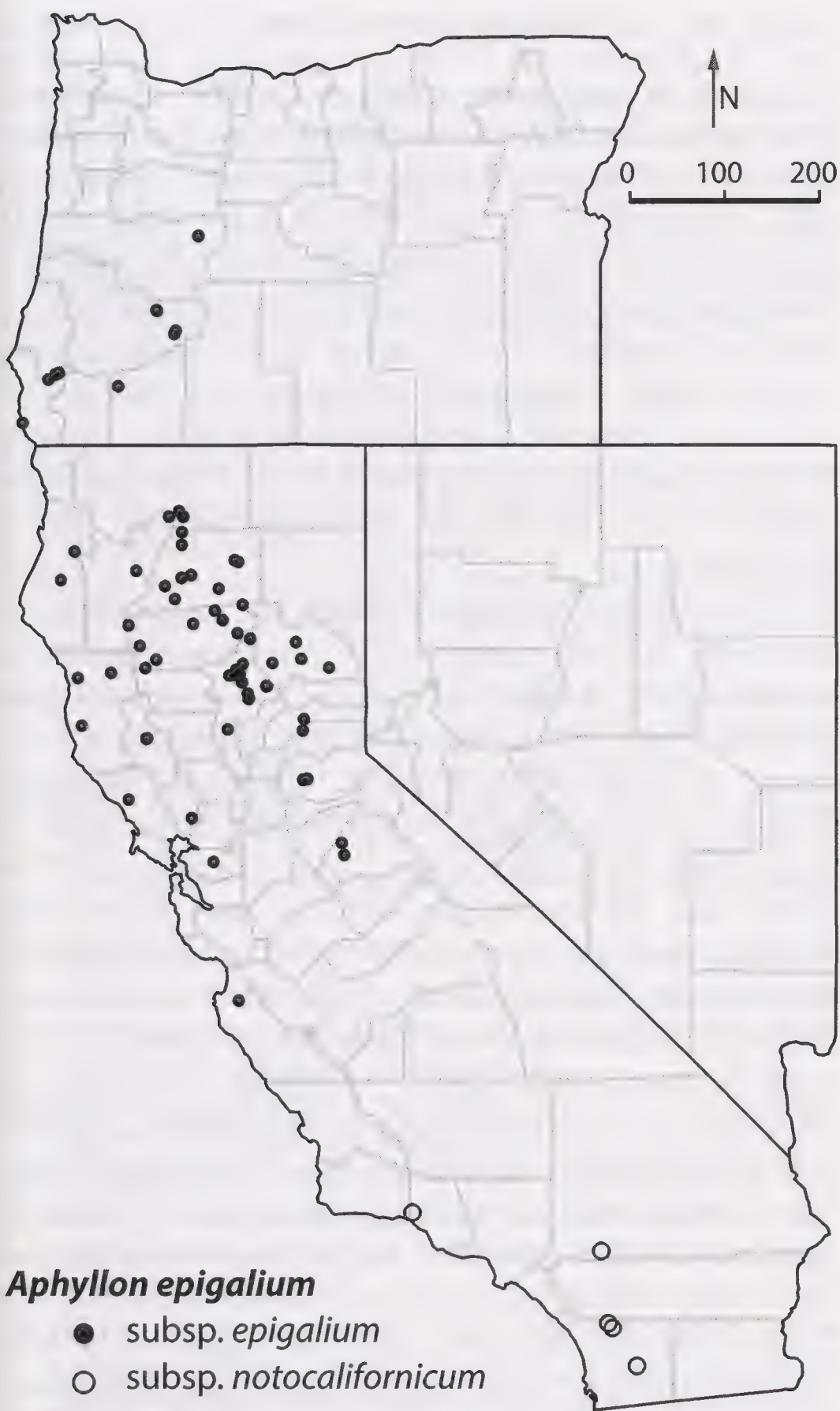


FIG. 3. Distribution of populations of *Aphyllon epigalium* in the western United States, with county boundaries shown in gray. Filled circles represent vouchered locations of *A. e.* subsp. *epigalium*. Open circles represent vouchered populations of *A. e.* subsp. *notocalifornicum*. Scale bar represents distance in kilometers.

Differing host associations between the two subspecies of *Aphyllon epigalium* appear to be consistent, even when the host of one subspecies is sympatric with the other parasite subspecies. For example, although the two subspecies are separated by a 330 km (200 mile) disjunction, from Merced County (the southern limit of subsp. *epigalium*), to the Santa Ynez Mountains in eastern Santa Barbara County (the northwestern limit of subsp. *notocalifornicum*) (See Fig. 3), some hosts overlap the range of both subspecies. Most strikingly, *Galium andrewsii*, the host of subsp. *notocalifornicum*, is abundant through-

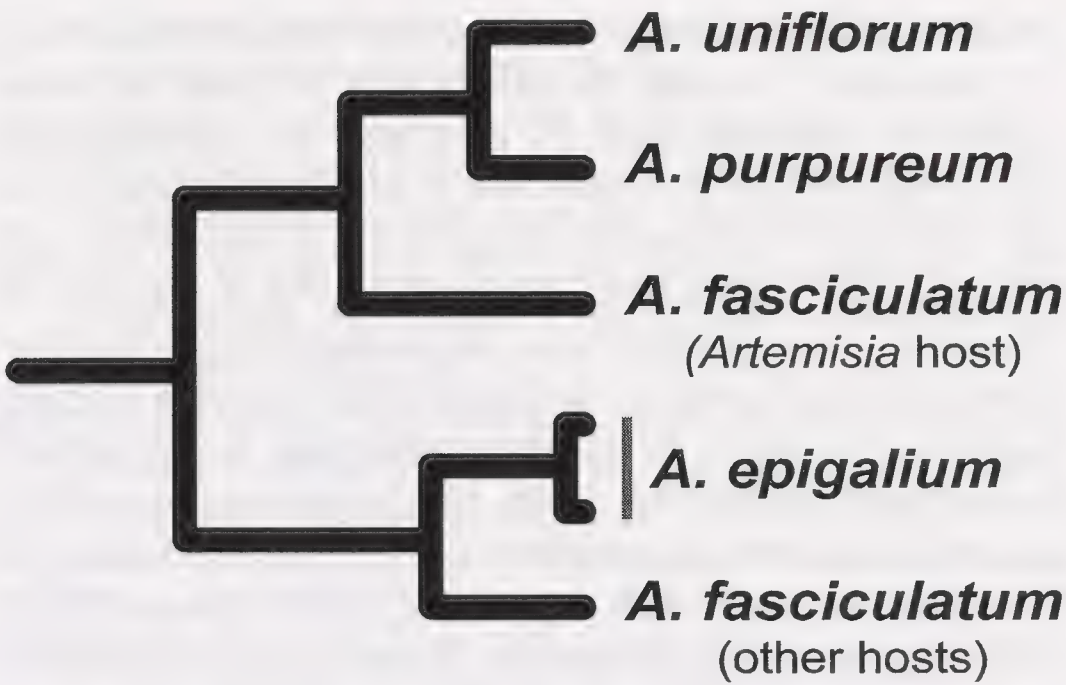


FIG. 4. Accepted phylogenetic relationships of all currently recognized taxa within *Aphyllon* sect. *Aphyllon*, including both subspecies of *A. epigalium*. All branches shown are strongly supported by ITS, ETS, and plastid DNA sequence data, posterior probability ≥ 0.97 . (Adapted from Schneider et al. 2016, Figs. 1–2).

out the inner Coast Ranges and has been collected as far north as 40° N, in Tehama County, CA. Although the distribution of this taxon overlaps considerably with that of subsp. *epigalium* throughout the North Coast Range, *G. andrewsii* is not a known host of *A. epigalium* subsp. *epigalium* even though it is very closely related to the other fleshy-fruited *Galium* species that are parasitized (Soza and Olmstead 2010). Similarly, we expect subsp. *notocalifornicum* to parasitize *G. californicum*, a host of subsp. *epigalium* that occurs within its southern California range, but no such association has yet been observed.

At even finer scales, differential host preference (or differential susceptibility on the part of host plants) may be occurring within populations. For example, in populations of *Galium*, certain individuals will be heavily infected by *Aphyllon epigalium*, while neighboring plants have no parasite load. In one population of *Galium bolanderi*, a dioecious host species, *A. epigalium* subsp. *epigalium* appeared to preferentially parasitize female host plants (A. E. L. Colwell, personal observation).

Abiotic Constraints

In regions where *A. epigalium* is present and a host is widespread, populations of *A. epigalium* nevertheless tend to be small and highly localized to pockets of unique plant communities within a larger matrix of conifer forest or chaparral (Fig. 2G, I). This suggests that other environment factors, such as host/habitat stability contribute to the scattered distribution of parasite occurrences. For example, fire regime may

Aphyllon epigalium subsp. *epigalium* with host (Yosemite National Park, Tuolumne Co., CA). F. Flower of *Aphyllon epigalium* subsp. *epigalium* at anthesis, frontal view (Carr 1559, OSC, photo courtesy of Gerald D. Carr). G. Type locality of *Aphyllon epigalium* subsp. *notocalifornicum*, Agua Tibia Wilderness, San Diego Co., CA. H. Habitat of *Aphyllon epigalium* subsp. *epigalium* in a *Sequoiadendron giganteum* (Lindl.) J. Buchholz grove. Blue arrow indicates collection site Colwell & Coulter 04-83 (YM). I. Habitat of *Aphyllon epigalium* subsp. *notocalifornicum* in a *Pseudotsuga macrocarpa* grove surrounded by chaparral, Santa Ynez Mountains, Ventura Co., CA. Blue arrow indicates collection site of Schneider 1033 (JEPS, SBBG).

enhance the distribution of *A. epigalium* either directly or mediated through its effects on its host in some habitats. Germination in response to exposure to smoke absorbed in water has been demonstrated for the related *Orobanche aegyptiaca* (Nun Bar and Mayer 2005). Similarly, charred wood is known to stimulate the germination of *Galium angustifolium*, which is closely related to known host species (Keeley and Keeley 1987). In the Sierra Nevada, low-intensity burns are associated with the regeneration of *G. sparsiflorum*, but more severe burns lead to declines in cover of this species (Knapp et al. 2007; Rocca 2009). In the central Sierra Nevada, flowering individuals of *A. epigalium* were observed by the first author to be more numerous following low intensity prescribed burns in the region's sequoia groves, although whether in this case it was due to host becoming more abundant, or to a direct germination response of the parasite to smoke is not known.

In other contexts, fire may limit the distribution of *A. epigalium*. A study of post-fire vegetation regeneration in the Santa Ynez Mountains found that *G. andrewsii* was sprouting in unburned areas, but not observed in burned areas during the two years post-fire (Christiansen and Muller 1975). It may be the case that this *Galium* species behaves as a fire-avoider in chaparral habitat. Thus, it is notable that the population of *A. epigalium* subsp. *notocalifornicum* from the Santa Ynez Mountains was not found in the chaparral, but in a small grove of *Pseudotsuga macrocarpa* surrounded by chaparral (Fig. 2I). This host-parasite combination may be utilizing a mesic microhabitat within the more widespread chaparral community of this region, and presence of the parasite could indicate a long history of stable host presence in this particular area. In either case, fire may play a key role in the robustness and distribution (e.g., patchiness) of parasite occurrences.

Conservation Status

Aphyllon epigalium subsp. *epigalium* is known from approximately 100 locations distributed widely across California and Oregon. However, the size of each population is small, typically fewer than twenty flowering individuals clustered around relatively few host plants, and thus each population is vulnerable to local extirpation. On the other hand, each capsule can produce thousands of seeds and studies of *Orobanche* indicate a long-term persistence of seed banks (Murdoch and Kebeab 2013). Therefore, we suggest that this species be evaluated for rarity regionally.

In contrast, *A. epigalium* subsp. *notocalifornicum* is currently known from only five populations in southwestern California. Two of these populations (Ocean View Trail, Santa Ynez Mountains, and along the trail to Eagle Peak, Cleveland National Forest) were confirmed extant by the last author in June 2016 (Schneider 1029, 1033; Fig. 2B, C). The third site, discovered in 1995 at the Fry Creek Campground on Palomar Mountain, was visited in 2016 but no individuals of *A. epigalium* were found. A fourth population was recorded in the early 20th century from Mill Creek, probably in vicinity of Mentone in the San Bernardino Mountains. The fifth and southernmost population near Cuyamaca Lake, San Diego County, was last collected in 1937. Given the wide distribution of its only known host, *Galium andrewsii*, within California and south to Sierra San Pedro Martír, Mexico, and the large distances between these five recorded populations, additional, undiscovered populations of *A. epigalium* subsp. *notocalifornicum* are expected to exist. Nevertheless, we recommend that this subspecies be considered for rare plant ranking.

KEY TO APHYLLON SECT. APHYLLON
IN WESTERN NORTH AMERICA

1. Flowers (3–)6–20 per stem; distal pedicels typically shorter than the stem (the combined vegetative and inflorescence axis); proximal pedicels as long as or rarely somewhat longer than the stem; hosts *Artemisia* L., *Eriodictyon* Benth., *Eriogonum* Michx., *Eriophyllum* Lag., *Phacelia* Juss. *A. fasciculatum*
- 1'. Flowers 1–4 per stem; distal pedicels as long or longer than the stem; proximal pedicels much longer (usually 2–3×) than the stem; hosts not as above
2. Flowers 1–2 per stem; corollas white to purple; corolla lobe margins ciliolate; palatal folds sometimes yellow; calyx lobes attenuate-filiform; hosts *Sedum* spp., Saxifragaceae, Apiaceae, Asteraceae
. *A. purpureum* (*Orobanche uniflora* L. subsp. *occidentalis* [Greene] Abrams ex Ferris)
- 2'. Flowers (1–)2–4 per stem; corollas cream to yellow, sometimes tinged pink or purple; corolla lobe margins glandular hairy; palatal folds concolor; calyx lobes narrowly triangular; hosts *Galium* spp. *A. epigalium*
3. Corollas yellow, often tinged reddish or purplish externally, (17–)20–30 mm long; corolla lobes spreading, length to width ratio < 2; hosts *Galium* spp. (but not *G. andrewsii*); southern Oregon to central California *A. epigalium* subsp. *epigalium*
- 3'. Corollas straw-color with pink or lavender cast externally, 13–20(–23) mm long; corolla lobes erect to slightly recurved at tip, length to width ratio ≥2; host *Galium andrewsii*; southern California.
. *A. epigalium* subsp. *notocalifornicum*

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